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Gas Exchange Characteristics of Wheat Stands Grown in a Closed, Controlled Environment

Raymond M. Wheeler,* Kenneth A. Corey, John C. Sager, and William M. Knott

ABSTRACT

Information on gas exchange of crop stands grown in controlled environments is limited, but is vital for assessing the use of crops for human life-support in closed habitats envisioned for space. Two studies were conducted to measure gas exchange of wheat stands (*Triticum aestivum* L. cv. Yecora Rojo) grown from planting to maturity in a large (20 m^2 canopy area), closed growth chamber. Daily rates of dark-period respiration and net photosynthesis of the stand were calculated from rates of CO_2 build-up during dark cycles and subsequent CO_2 drawdown in the light (i.e., a closed-system approach). Lighting was provided as a 20-h photoperiod by high-pressure sodium lamps, with canopy-level photosynthetic photon flux density (PPFD) ranging from 500 to 800 $\mu mol\ m^{-2}\ s^{-1}$ as canopy height increased. Net photosynthesis rates peaked near 27 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ at 25 d after planting, which corresponded closely with stand closure, and then declined slowly with age. Similarly, dark-period respiration rates peaked near 14 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ at 25 d and then gradually declined with age. Responses to short-term changes in irradiance after canopy closure indicated the stand light compensation point for photosynthesis to be near 200 $\mu mol\ m^{-2}\ s^{-1}$ PPFD. Tests in which CO_2 concentration was raised to $\approx$2000 $\mu mol\ mol^{-1}$ and then allowed to draw down to a compensation point showed that net photosynthesis was nearly saturated at >1000 $\mu mol\ mol^{-1}$; below $\approx$500 $\mu mol\ mol^{-1}$, net photosynthesis rates dropped sharply with decreasing CO_2. The CO_2 compensation point for photosynthesis occurred near 50 $\mu mol\ mol^{-1}$. Short-term (24 h) temperature tests showed net photosynthesis at 20 °C $\geq$ 16 °C > 24 °C, while dark-period respiration at 24 °C > 20 °C > 16 °C. Rates of stand evapotranspiration peaked near Day 25 and remained relatively constant until about Day 75, after which rates declined slowly. Results from these tests will be used to model the use of plants for CO_2 removal, O_2 production, and water evaporation for controlled ecological life support systems proposed for extraterrestrial environments.

NUMEROUS STUDIES of plant gas exchange have been conducted over the past 30 yr, often with the assistance of sophisticated mobile laboratories in the field (15). Most of these studies have focused on single-leaf measurements; consequently much less is known about gas exchange at the stand or community level, where multiple layers of leaves, nonphotosynthetic organs, and the rhizosphere are included. Musgrave and Moss (27) made one of the first attempts to enclose plant stands in the field to measure gas exchange. Studies since then have used various configurations and techniques to monitor gas exchange rates of agronomic and natural plant stands (2,11,16,22). To obtain further environment control for plant stand gas exchange measurements, sunlit chambers have been developed for use in greenhouses (1,20), while a variety of smaller chambers with more rigorous environmental control and electrical lighting have been developed for use in the laboratory (6,12,17,23). However, few of these sytems have been used to track gas exchange throughout the entire life cycle of plants, and fewer still are capable of enclosing stands larger than 1 m^2.

Gas exchange of large stands of plants is of particular interest with regard to utilizing plants for human life support systems for long durations in space (32). Through photosynthesis, plants would remove CO_2 accumulated from human respiration, while releasing O_2 back to the human habitat. In addition, transpired water from the plants could be condensed from the atmosphere to provide a source of clean water. To test this concept, a large, sealed plant growth chamber was constructed to gather baseline information with selected crops. The large size was deemed necessary to address scale-up problems that might not be encountered in the laboratory or standard growth chambers, while the tight closure provided the capability to accurately monitor system mass flows (gases, water, and nutrients) and any potential problems from contaminant build-up (e.g., organic volatiles from construction materials and plants). We report here on tests in which the gas exchange of two 20-m^2 wheat stands was monitored from early vegetative development through harvest.

MATERIALS AND METHODS

Chamber Description

Studies were conducted in a cylindrical steel chamber that formerly served as a hypobaric test vessel at Kennedy Space Center, FL. The chamber was 3.5 m in diameter and 7.5 m high, and divided into two levels, with two plant-growing shelves in each level. Each of the four shelves supported 16 plastic (PVC) trays, 0.25 m^2, thereby providing a total planted area of 16 m^2. After accounting for gaps between trays and the tendency of shoots to extend beyond the edges of the trays, total stand (canopy) area at full development was estimated to be 20 m^2. Using calculations from mechanical drawings and concentration changes from measured additions of CO_2 gas, the entire atmospheric volume of the chamber, including air ducting, was estimated to be 112.6 m^3.

Lighting System

Lighting for plant growth was provided by 96 high-pressure sodium lamps (400-W) separated from the plants by Pyrex glass barriers. All lamps were operated with externally mounted dimming ballasts (Wide-Lite, San Marcos, TX), providing PPFD levels from $\approx$650 $\mu mol\ m^{-2}\ s^{-1}$ (at full power) to $\approx$50 $\mu mol\ m^{-2}\ s^{-1}$ (at the lowest dimming set point) at tray level, which was $\approx$0.6 m below the lamp barrier. At 0.1 m below the lamp barriers, PPFD levels near 1000 $\mu mol\ m^{-2}\ s^{-1}$ could be attained, but distribution was less uniform.

Heat Exchange System

Air circulation was provided by two 30-kW blowers (one for each level), with motors mounted external to the air ducts to minimize possible contaminants from electrical and lubri-

R.M. Wheeler, J.C. Sager, and W.M. Knott, NASA Biomedical Operations and Research, Mail Code MD-RES, Kennedy Space Center, FL 32899; and K.A. Corey, Dep. of Plant and Soil Sci., Univ. of Massachusetts, Amherst, MA 01003. Received 2 Dec. 1991. *Corresponding author.

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Abbreviations: CER, carbon dioxide exchange rate; ET, evapotranspiration; PAR, photosynthetically active radiation; PPFD, photosynthetic photon flux density; PVC, polyvinyl chloride; VPD, vapor pressure deficit.

Table 1. Environmental parameters for controlled-environment, closed-system gas exchange studies of wheat stands.

Study	Temperature		Relative Humidity		VPD†		CO_2‡		PPFD§
	light	dark	light	dark	light	dark	light	dark	
	°C		%		kPa		μmol mol^{-1}		μmol m^{-2} s^{-1}
First	20.2	16.8	81	84	0.42	0.31	1160	1293	549
Second	20.1	16.4	72	78	0.66	0.41	1098	1273	691

† Water vapor pressure deficit between leaves and air, assuming leaves and air at same temperature.
‡ CO_2 controlled to near 1000 μmol mol^{-1} during the light cycle.
§ PPFD = photosynthetic photon flux density, averaged from weekly measurements at canopy level.

cated components. The air-handling systems provided from three to four air exchanges per minute (400 m^3 min^{-1}), with air velocities from 0.2 to 1.5 m s^{-1} at the plant canopy level. Heat rejection and humidity control were provided by chilled-water coils positioned after each blower. Condensate that formed on the cold coils was collected in stainless steel holding tanks, providing a direct measure of evapotranspiration from the chamber. When needed, supplemental humidification was provided by atomized streams of deionized water sprayed directly into the air ducts. Air streams for both air-handling systems were filtered on each pass with a coarse particulate filter and a high-efficiency particulate filter (0.3 μm).

Nutrient Delivery System

Plants for both studies were grown using nutrient film technique (9), with the nutrient solution circulated continuously to the trays (≈1 L min^{-1} tray^{-1}) from reservoirs located outside the chamber. Separate PVC plumbing and reservoirs were used for each of the four shelves, with headspaces of each reservoir vented back to the main growing chamber. Nutrient solutions were a modified half-strength Hoagland with NO_3 as the only N source (21). Solution pH for each of the four systems was automatically maintained at 6.0 using 0.4 *M* HNO_3, while solution electrical conductivity was automatically maintained near 0.12 S m^{-1} with additions of a concentrated, complete stock solution.

Atmospheric Monitoring and Control

Carbon dioxide concentrations were monitored using three infrared gas analyzers (Anarad AR-200, Santa Barbara, CA), with all gas sample streams being returned to the chamber. Once each day, all analyzers were automatically calibrated against standard gases ranging near 0, 500, 1000, and 2000 μmol mol^{-1} (ppm) CO_2. Oxygen concentrations were monitored but not controlled, using fuel-cell detectors plumbed in series with the infrared analyzers. Oxygen detectors were calibrated against air obtained outside the building, assuming a constant 209 mmol mol^{-1} (20.9%) O_2 concentration. On several occasions for the second study, CO_2 added to the chamber was monitored using mass flow sensors (Brooks Instruments series 5860E, Hatfield, PA).

Air temperatures and relative humidity were monitored and controlled using sensors (General Eastern model 455, Watertown, MA) mounted in a plenum located after the heat exchangers and air filters. Redundant temperature and humidity sensors (Vaisala model HMP 111, Helsinki, Finland) used strictly for monitoring were positioned at the top of the plant canopy on each growing shelf. Because of the large size of heat exchange coils and operation at less than full chilled water flow, small temperature gradients often existed in the air stream. This amounted to about 1 °C difference between the upper and lower growing shelves in each half of the chamber.

Plant Cultural Procedures

Two studies were conducted with Yecora Rojo wheat, in which plants were grown from seed to physiological maturity. Yecora Rojo was chosen because of its short height and high yield in previous controlled environment studies (5,6,7,32). Seeds were soaked for ≈ 1 hr in deionized water and then refrigerated at 4 °C for 24 h prior to sowing directly onto culture tray inserts, where they were supported by juxtaposing strips of polyethylene plastic mounted between plastic T-supports (29). This provided rows of seeds supported 4 to 5 cm above the flowing nutrient solution. Prewashed nylon fabric strips were placed between the plastic strips to act as a water wick for germinating seeds. Seeds were sown at a rate of ≈ 1500 m^{-2} to achieve high productivity (7). For the first 5 d in the first study and the first 4 d in the second study, trays were covered with white, translucent acrylic covers to maintain high humidity during seedling establishment. At 16 d, plastic support nets were positioned ≈ 16 cm above each tray to prevent lodging later in growth. Plants were harvested at maturity: Day 86 in the first study and Day 85 in the second study.

Environmental Conditions

The chamber was kept dark for the first 2 d after planting for both studies. For the remainder of each study, lamps were cycled to provide a 20-h light/4-dark photoperiod. Translucent acrylic germination covers kept over the trays reduced the incident PPFD by ≈85%, thus allowing ≈90 μmol m^{-2} s^{-1} PPFD to reach the seedlings. In the first study, lamps were dimmed on Day 28 to maintain ≈500 μmol m^{-2} s^{-1} PPFD, while lamps were kept at full power for the second study, providing ≈690 μmol^{-2} s^{-1} PPFD throughout growth (Table 1). Incident PPFD was measured with a quantum sensor (LI-COR LI-190, Lincoln, NE) by taking readings at the top of the canopy for each of the 64 trays at weekly intervals. In the second study, additional irradiance measurements were taken above and below the canopy at weekly intervals using a sunfleck ceptometer (Decagon Devices, Pullman, WA).

Temperatures for the first study were maintained near 23 °C (light and dark) until Day 20, followed by a constant 20 °C until Day 33, and finally a 20 °C/16 °C (light/dark) thermoperiod for the remainder of the study. For the second study, temperatures were maintained at 23 °C until Day 10, after which a 20 °C/16 °C thermoperiod was maintained. Carbon dioxide concentrations were maintained at 1000 μmol mol^{-1} throughout the light cycles for both studies. No attempts were made to suppress CO_2 increases during the dark cycles, nor to prevent O_2 build-up during the light cycles. Oxygen concentrations seldom exceeded 220 mmol mol^{-1} (22%; i.e., 1% above ambient), because the chamber was usually entered once daily for maintenance activities. Average temperature, humidity, water vapor pressure deficit, CO_2, and PPFD data for the two studies are shown in Table 1.

Gas Exchange Measurements

Carbon Dioxide

Because no attempts were made to suppress CO_2 build-up from respiration during dark cycles, CO_2 showed a repeating pattern of dark-period increase followed by a light-period (morning) drawdown back to the 1000 μmol mol^{-1} set point

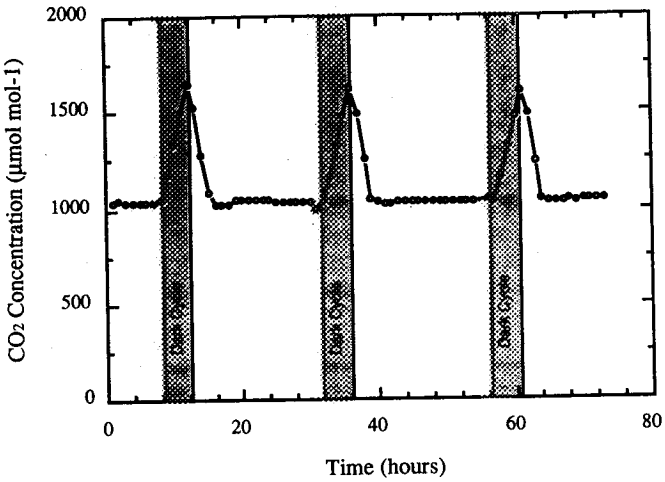

Fig. 1. Effect of diurnal light cycles on CO_2 concentrations with a wheat stand in a closed chamber. CO_2 was controlled at 1000 μmol mol^{-1} (ppm) during the 20-h light cycles (to offset stand photosynthesis) and allowed to rise (from stand respiration) during the 4-h dark cycles. Data were taken between 28 and 30 d after planting.

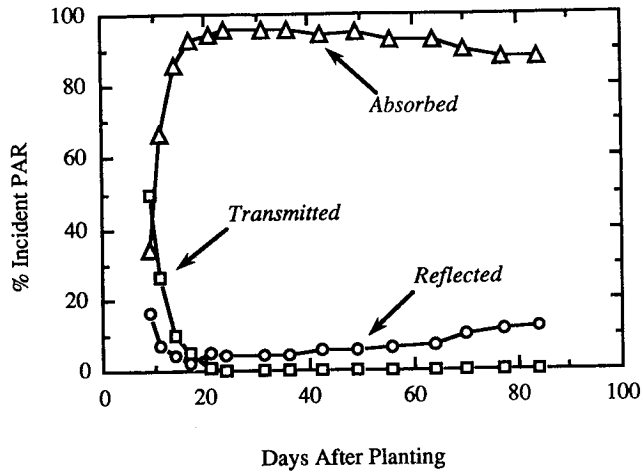

Fig. 2. Percent of incident photosynthetically active radiation (PAR) absorbed, transmitted, and reflected by a wheat canopy over time. PPFD averaged 691 μmol m^{-2}s^{-1} throughout growth.

(Fig. 1). At 1000 μmol mol^{-1}, CO_2 was added to the chamber as needed to maintain the set point. With the chamber tightly sealed and the atmospheric volume and stand area known, rates of CO_2 increase during the dark and the subsequent light-period drawdown could be used as a daily measure of stand respiration and photosynthesis, i.e. as in a closed gas exchange system. This assumes that (i) rates calculated from morning drawdown cycles were representative of rates throughout the day, and (ii) changes in CO_2 concentration above 1000 μmol mol^{-1} had no significant effect on stand respiration and photosynthesis.

To test the first assumption, (that morning photosynthetic rates were representative of the rate throughout the day), the rates of mass addition of CO_2 were monitored across the entire day of Days 35 and 50, while a series of sequential drawdowns (from ≈ 1500 to 1000 μmol mol^{-1}) were conducted throughout the light period on Day 36. In each case, photosynthetic rates were nearly constant across the light period, indicating that there were no pronounced diurnal changes in photosynthesis at these ages. To test the second assumption, daily CO_2 drawdowns were tested with regression analysis and found to be linear ($r^2 > 0.99$) over the 1000 to 2000 μmol mol^{-1} range; hence the effects of changing CO_2 concentration on photosynthetic rates over this range were considered negligible (10,35).

Tests to estimate chamber leakage rates were conducted prior to and following each study (without plants) by raising the CO_2 concentration to ≈ 2000 μmol mol^{-1} and tracking the concentration decay over time. Leakage rates ranged from 5 to 10% of the chamber volume per day (0.2 to 0.4% volume h^{-1}). Since gas exchange rates could be calculated from data sets of 1 to 2 h, leakage effects were ignored. For all gas exchange calculations, no data were taken from the first 20 min following the day–night or night–day transitions, to avoid transient pressure effects on gas analyzers resulting from temperatures changes in the chamber (up to 0.5 kPa during heating and −0.5 kPa during cooling)(35).

Water

Evapotranspiration rates from the plant stand were measured daily from the volume of condensate collected from the cold coils of the heat exchange system. Although culture trays were covered by plastic plant-support covers, air gaps existed between the covers and the edges of the trays, resulting in some direct evaporation. Prior to complete canopy cover by the plant near Day 22, direct evaporation from the nutrient solution delivery system probably accounted for a portion of the condensate production. After canopy closure, condensate production was assumed to represent stand transpiration. Because supplemental humidification was used for the first 14 d in the first study, data for condensate production did not accurately reflect stand evapotranspiration and are not reported.

All gas exchange rate calculations are expressed on a unit-area basis, assuming a total area of 20 m^2 available for canopy growth.

RESULTS

Growth and Development

Seedling establishment in the nutrient film system proceeded rapidly, with plant heights averaging 0.21 m and 0.24 m at Day 15 in the first and second studies, respectively. Canopy height increased nearly linearly after this time, reaching 0.55 m for both studies at Day 42, when growth essentially ceased. Heading was first noted at about Day 35 in both studies. At harvest on Days 85 and 86, stands were estimated to be physiologically mature, as determined by the loss of green color of the heads.

Measurements of above- and below-canopy PAR in the second study showed that canopy cover increased rapidly beginning ≈ 10 d after planting (Fig. 2). By Day 14, 86% of the incident PAR was absorbed by the canopy (Fig. 2). Canopy closure was assumed to be complete by Day 22, when 95% of the incident PAR was absorbed. Following canopy closure, PAR absorption remained relatively constant until about Day 50, after which canopy absorption decreased slightly and reflectance increased slightly. Although below-canopy measurements were not taken for the first study, visual observations indicated that canopy closure occurred at about the same time.

Stand CO_2 Exchange Rates

For both studies, stand net photosynthesis rates increased rapidly during early growth, peaking near 27 μmol CO_2 m^{-2} s^{-1} at 24 d after planting (Fig. 3) when

incident PPFD was ≈700 μmol $m^{-2}s^{-1}$ at the top of the canopy. At Day 28 in the first study, lamps were dimmed to maintain ≈500 μmol m^{-2} s^{-1} PPFD at the top of the canopy for the rest of the study; this dimming resulted in a 40% decrease in the rate of net photosynthesis to ≈15 μmol CO_2 m^{-2} s^{-1}. Except for the dimming event, photosynthesis rates remained relatively constant for both studies from Day 25 through 35 and the onset of heading, after which rates declined slowly through grain fill and canopy senescence (Fig. 3). In the second study with no dimming used, canopy-level PPFD continued to rise as plants grew, reaching ≈800 μmol m^{-2} s^{-1} near Day 45. Despite this, no increase in stand photosynthesis rates were noted after about Day 25, suggesting that aging or changes in canopy structure may have offset any benefit from the increase in canopy-level irradiance.

Dark-period respiration rates for both studies peaked at 13 to 14 μmol CO_2 m^{-2} s^{-1} at 24 days after planting (Fig. 3). Dark-period respiration rates for each study showed a gradual decline with age, beginning at about Day 30. On Day 33, dark-period respiration during the first study showed a slight drop, which coincided with the time when dark-period temperatures were lowered from 20 to 16 °C (Fig. 3). After this, respiration rates from the first study remained slightly lower than rates from the second study.

Points deviating from the general trends in photosynthesis and respiration shown in Fig. 3 usually reflect days when environmental tests were conducted (e.g., PPFD or temperature comparisons).

PPFD Effects

On several occasions in both studies, the effect of PPFD on stand photosynthesis was determined. Carbon dioxide concentrations were raised to near 2000 μmol mol^{-1} and allowed to be drawn down while the lamps were dimmed to different levels. The rates of CO_2 drawdown were greater at higher PPFD levels (Fig. 4). Changing the order of irradiance treatments did not affect the resultant drawdown rates (35). When lamps were dimmed to very low levels after canopy closure, CO_2 concentrations within the chamber increased, indicating that the PPFD was below the compensation point. A typical comparison of CO_2 exchange rate vs. PPFD shows a linear increase in stand photosynthesis as PPFD was increased to ≈800 μmol m^{-2} s^{-1} and a PPFD (light) compensation point near 200 μmol m^{-2} s^{-1} (Fig. 4). The PPFD compensation points averaged 190 μmol m^{-2} s^{-1} (from Day 35 to 75) in the first study and 210 μmol m^{-2} s^{-1} (from Day 16 to 70) in the second study. A test conducted at Day 84 in the second study showed that the PPFD compensation point increased to >300 μmol m^{-2} s^{-1} just prior to harvest.

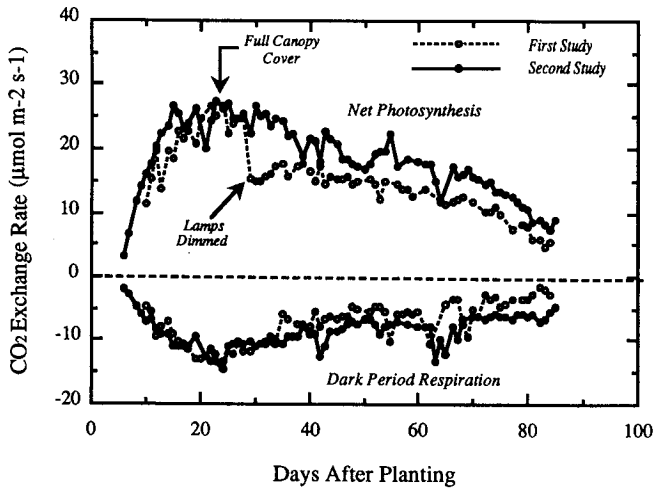

Fig. 3. CO_2 exchange rates over time for two stands of wheat grown in a closed chamber. CO_2 uptake (net photosynthesis) rates during the 20-h daily light cycle are shown as positive values, while CO_2 production (respiration) rates during the 4-h daily dark cycle are shown as negative values. Full canopy cover occurred at about Day 22 and heading was first apparent at about Day 35. During the first study, lamps were dimmed to maintain 500 μmol m^{-2} s^{-1} PPFD at Day 28; lamps were maintained at full power throughout the second study.

CO_2 Effects

On several occasions in both studies, CO_2 concentrations were raised above 1500 μmol mol^{-1} and then allowed to be drawn down entirely to the compensation point (10,35). These continuous drawdowns typically lasted from 8 to 10 h with full lighting, depending on stand age. In all cases, the pattern of drawdown showed a near linear decrease until CO_2 fell below 1000 μmol mol^{-1}, after which the CO_2 decreased at a decreasing rate (Fig. 5). Taking the first derivative of the drawdown curves showed that stand net photosynthesis increased only slightly at CO_2 concentrations above 1000 μmol mol^{-1}, indicating the CO_2 effect on photosynthesis was nearly saturated (Fig. 5). Below ≈ 500 μmol mol^{-1}, photosynthesis decreased sharply, with a CO_2 compensation point typically occurring near 50 μmol mol^{-1}.

Temperature Effects

On several occasions during each study, temperatures were held at 16, 20, or 24 °C for a 24-h period and rates

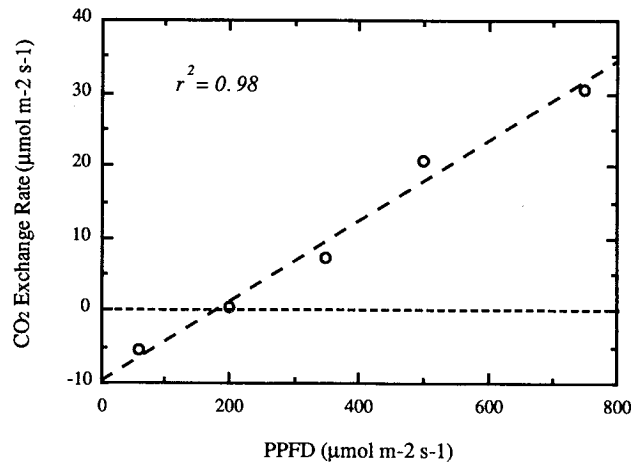

Fig. 4. Effect of photosynthetic photon flux density (PPFD) on CO_2 exchange rate (CER) by a stand of wheat in a closed chamber. CER showed a linear response over the range of PPFD levels tested (max. ≈ 750 μmol $m^{-2}s^{-1}$), with a compensation point near 190 μmol $m^{-2}s^{-1}$. Data were taken at 41 d after planting.

of net photosynthesis and dark-period respiration of the stand were monitored. For all tests, dark-period respiration showed a distinct increase with increased temperature (Fig.6). Although absolute rates varied somewhat with age, stand net photosynthesis at 20 °C ≥ 16 °C > 24 °C (Fig. 6). As plants aged, rates of net photosynthesis were affected less by temperature changes between 16 and 24 °C.

Stand Evapotranspiration

Evapotranspiration followed a trend similar to that of stand CO_2 uptake, showing a rapid rise during early growth and peaking near canopy closure at 100 L d^{-1} (5 L m^{-2} d^{-1}) for the first study and 120 L d^{-1} (6 L m^{-2} d^{-1}) for the second study (Fig. 7). After Day 25, rates showed a gradual decline until Day 75, after which rates declined rapidly to ≈ 3 L m^{-2} d^{-1} at Day 85. Stand evapotranspiration rates from the first study were slightly less than rates from the second study, possibly reflecting the influence of the lower water vapor pressure deficit and lower PPFD in the first study (Table 1). In general, evapotranspiration rates did not decline as markedly over time as did CO_2 exchange rates.

DISCUSSION

CO_2 Exchange

With the capability of growing large plant stands in an atmospherically sealed chamber, gas exchange rates were monitored throughout growth and development of a wheat crop using a closed-system approach. Time-course records of photosynthesis showed that peak rates of CO_2 uptake occurred early in growth, soon after full canopy cover was established (Fig. 3), similar to results reported from field studies (30). In our controlled environment studies, peak photosynthetic rates occurred well before heading was apparent, whereas field measurements indicate that peak rates may not occur until heading and anthesis (16). In smaller-scale, controlled environment studies, Gerbaud et al. (17) reported that peak photosynthetic rates for a wheat canopy occurred between 70 to 80 d after planting; however, their study used a relatively low population of 80 plants m^{-2} as compared to ≈ 1500 plants m^{-2} in our studies. Thus the different results might be explained by the different times required to reach canopy closure and maximum PAR interception. The close relationship between canopy gas exchange and PAR interception has also been shown in field studies (30,31,34).

As with photosynthesis, dark-period respiration rates peaked very early in development and then decreased with time (Fig. 3). Similar results have been reported from field studies (31), suggesting a diminishing role for growth respiration over time (33). At harvest, total stand biomass was greater in the second study, where higher PPFD levels were maintained throughout growth. From Day 35 until harvest, respiration rates were higher in the study with the higher PPFD. This could have been a result of higher carbohydrate reserves from higher diurnal photosynthetic rates noted in the second study, or it may reflect a higher standing biomass and higher maintenance respiration throughout this period in the second study.

In both studies, the rate of CO_2 increase was linear over the entire dark period (CO_2 concentrations ranging from 1000 to 2000 μmol mol^{-1}), and hence stand respiration was constant. This contrasts with reports indicating that elevated CO_2 (340 vs. 680 μmol mol^{-1}) can decrease respiration (8,19), and suggests that there may be little additional effect of CO_2 on respiration above concentrations of 1000 μmol mol^{-1}; however, further testing is needed to determine if and where CO_2 effects on respiration become saturated. The linear rates throughout the dark indicate that respiration was not carbohydrate-limited across the 4-h cycle, but no direct measurements were made to verify this.

PPFD Effects

Results from the dimming tests emphasize the strong influence of PPFD on stand photosynthetic rates. The linear increase in CO_2 uptake up to 800 μmol m^{-2} s^{-1} PPFD indicates that this was still well below light saturation and is consistent with previous reports showing

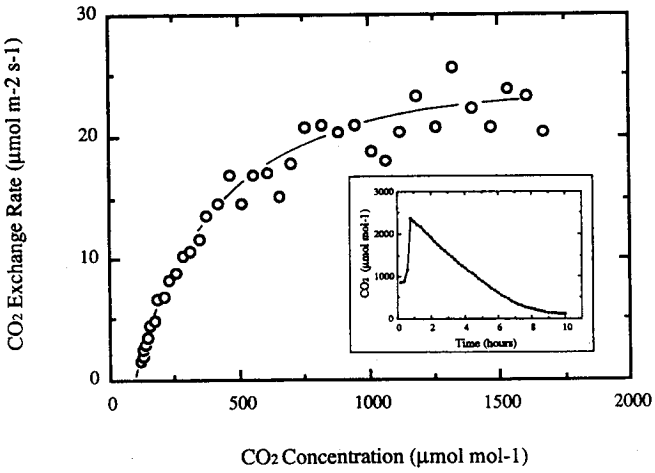

Fig. 5. CO_2 exchange rate by a stand of wheat in a closed chamber in response to changing CO_2 concentration. Data were calculated from a single drawdown test lasting ≈ 10 h (shown in inset).

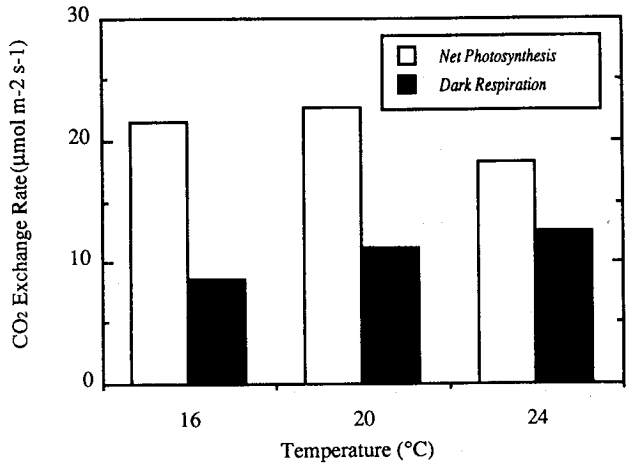

Fig. 6. Effect of temperature on CO_2 exchange rates by a stand of wheat in a closed chamber. Data were taken between 42 and 44 d after planting.

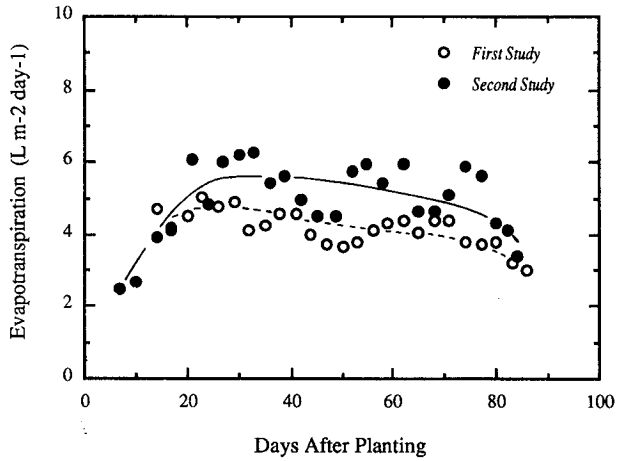

Fig. 7. Evapotranspiration rates over time for two stands of wheat grown in a closed chamber. Data were calculated from condensate water collected from the cold coils of the atmospheric heat exchange system. Values prior to Day 15 in the first study were not included because water was added for supplemental humidification.

the capacity of high-density wheat stands to utilize high levels of PAR (7). Over a 20-h photoperiod, 800 μmol m^{-2} s^{-1} would provide 59 mol m^{-2} d^{-1}, a value similar to many wheat fields on a clear summer day. Yields of wheat grown in controlled environments have been shown to increase up to 2080 μmol m^{-2} s^{-1} PPFD for 20 h d^{-1} (150 mol m^{-2} d^{-1}), a value far exceeding maximum field irradiance (7).

The PPFD (light) compensation point for the stands after canopy closure averaged 190 μmol m^{-2} s^{-1} in the first study and 210 μmol m^{-2} s^{-1} in the second study. These values are much higher than those reported for single leaves (e.g., 10–20 μmol m^{-2} s^{-1})(4). This discrepancy can be explained by the higher background respiration rates for a canopy, compared with single leaves. Wheat stands grown at even higher PPFD levels (e.g., 2000 μmol m^{-2} s^{-1}) with a very large standing biomass have shown PPFD compensation points as high as 600 μmol m^{-2} s^{-1} (5). The notion that stand PPFD compensation points are determined by background respiration is supported by tests showing that low temperatures can be used to decrease PPFD compensation points (5).

In the first study, lamps were dimmed from near 700 μmol m^{-2} s^{-1} to $\approx$500 μmol m^{-2} s^{-1}, a decrease of $\approx$29% in PPFD, which resulted in a 40% decrease in net photosynthesis from (25 to 15 μmol CO_2 m^{-2} s^{-1}). By estimating dark respiration of 11 μmol CO_2 m^{-2} s^{-1} (Fig. 4), one can then estimate gross photosynthesis to be $\approx$36 μmol CO_2 m^{-2} s^{-1} (25 + 11) before dimming and about 26 μmol CO_2 m^{-2} s^{-1} $\approx$(15 + 11) after dimming. Although a 29% decrease in PPFD appeared to cause a disproportionately large decrease in net photosynthesis, it closely matched the decrease in stand gross photosynthesis.

When net photosynthesis rates peaked at 27 μmol m^{-2} s^{-1} during rapid vegetative growth, incident PPFD was $\approx$700 μmol m^{-2} s^{-1}; thus, the quantum efficiency for net photosynthesis during rapid vegetative growth equaled 0.04 mol CO_2 mol^{-1} PAR. Assuming all the CO_2 fixed was stored as carbohydrate, CH_2O, this would yield [0.04 mol CH_2O] $\times$ [30 g mol^{-1}], or 1.2 g biomass mol^{-1} PAR. This peak value is relatively high, but not unexpected for wheat grown hydroponically with CO_2 enrichment (7). On an energy basis, if wheat biomass contains 17.2 kJ g^{-1} (7) and the energy of PAR from high-pressure sodium lamps is $\approx$200 kJ mol^{-1}, then energy conversion of PAR into biomass during peak growth would equal [(1.2 g mol^{-1} PAR) $\times$ (17.2 kJ g^{-1})] / [200 kJ mol^{-1} PAR], or 10.3%. This value compares closely with a peak energy conversion rate of 9.9% reported from other controlled environment studies with wheat (17).

CO_2 Effects

Complete CO_2 drawdown tests showed a photosynthetic response to CO_2 concentration typical for most C_3 plants: Only a small decrease in photosynthetic rate was noted as CO_2 was decreased from 1500 μmol mol^{-1} to $\approx$1000 μmol mol^{-1}, while decreasing the CO_2 further to $\approx$500 μmol mol^{-1} caused an increasingly steeper drop in photosynthetic rate. Decreasing the CO_2 below 500 μmol mol^{-1} caused a sharp drop (Fig. 5), indicating the importance of maintaining CO_2 above 500 μmol mol^{-1} (at 210 mmol mol^{-1} O_2) for sustaining high photosynthetic rates. Related growth chamber studies with wheat have also shown large differences in stand gas exchange between 330 and 660 μmol mol^{-1} CO_2 (13). Whether CO_2 concentrations much greater than 1500 μmol mol^{-1} would adversely affect stand gas exchange and productivity (i.e., become toxic) will require further study. In subsequent studies with soybean using a 14-h dark period (data not shown), we have not noticed any obvious effects on stand photosynthetic drawdowns, even with CO_2 concentrations starting near 2800 μmol mol^{-1}.

The CO_2 drawdowns demonstrate a powerful test that can be performed in a closed system: entire CO_2 response curves for stand photosynthesis can be obtained in a short time. This assumes, however, that the plant stand continually adjusts to the changing CO_2 concentrations. Evidence from single-leaf measurements suggests that even the most rapid drawdown rates of 2 μmol mol^{-1} min^{-1} from our tests are sufficiently slow to allow plant adjustment (26). In addition, tests comparing segments of CO_2 drawdowns with steady-state measurements (using CO_2 mass flow calculations) taken at different CO_2 concentrations indicate that drawdowns did indeed give accurate measurements of stand photosynthetic response across the entire range of CO_2 concentrations (10).

Results from several complete CO_2 drawdowns in these studies along with subsequent studies with soybean (also C_3) indicate that the stand CO_2 compensation points were generally near 50 μmol mol^{-1}, values not much different from those measured for single leaves (3,18) and whole plants (18). This contrasts with the large difference between stand and leaf PPFD compensation points noted earlier. Assuming the atmosphere is well mixed, when a CO_2 compensation point is reached where CO_2 concentration is limiting photosynthesis, any CO_2 contributed from biomass respiration should be accounted for in the measured atmospheric concentration. Hence, leaves should not differ much from whole stands. But when light compensation is reached where PPFD is limiting photosynthesis, any CO_2 from biomass respiration detracts from net CO_2 uptake, resulting in PPFD compensation points being higher for stands than for single leaves. In the case of irradiance, gradients exist across the profile of stands but not for single leaves. If one could

imagine a stand composed entirely of leaves (i.e., no nonphotosynthetic organs) with light uniformly distributed within the stand, then stand PPFD compensation points should be similar to those of single leaves.

Temperature Effects

Raising the temperature from 16 to 20 or 24 °C caused a distinct increase in dark-period respiration rates. If a dark period is used in the growing of wheat (and note that continuous light can be used; see 5,6), our results indicate that 16 °C would be preferable to 20 or 24 °C, to minimize C loss from the stand. Whether this is true throughout growth needs further testing. Slowing respiration during dark cycles, especially during early growth and development, may slow necessary metabolic and developmental events (25), which would be detrimental to achieving maximum growth.

The effects of temperature on net photosynthesis were not as pronounced as the effects on dark-period respiration. By combining dark-period respiration and net photosynthesis rates in Fig. 6, one can estimate gross photosynthesis to have peaked near 20 °C. In a study comparing 17,20, and 23 °C, Bugbee (5) showed that gross photosynthesis rates and quantum efficiences for Yecora Rojo wheat were highest at 23 °C, but reduction in dark respiration at 17 °C offset this, resulting in highest yields at 17 °C. Our net CO_2 uptake tests showed a trend consistent with those yield results, where 20 °C was equal or slightly perferable to 16 °C, and 24 °C was the least desirable.

Evapotranspiration

Unlike CO_2 exchange rates, evapotranspiration rates by the stand did not show as pronounced a decline with age. However, peak ET rates occurred near the same time that peak photosynthetic rates occurred, about the time of canopy closure (Fig. 3 and 7). Gerbaud et al. (17) reported peak transpiration rates near 8 to 9 L m^{-2} d^{-1}, while rates in our studies peaked near 5 to 6 L m^{-2} d^{-1}. The differences might be explained by differences in water vapor pressure deficit between the two studies, although precise humidity and VPD data were not available for comparison.

The volumes of condensate recovered emphasize that water vapor is by far the major gas passing through the chamber atmosphere: 100 L (100 kg) of liquid water condensed each day (Fig. 7) would correspond to (100 kg)/(0.018 kg mol^{-1}) × (24 L mol^{-1}) at 20 °C, or ≈130 000 L (130 m^3) of water vapor at 20 °C. Thus despite the chamber being closed, a volume of water vapor exceeding the entire volume of the chamber (113 m^3) was removed from the system each day by the cold coils.

Peak canopy ET rates of 6 L m^{-2} d^{-1} (Fig. 7) would equate to a continuous short-term rate of 3.8 mmol H_2O m^{-2} s^{-1}. Knowing that this occurred at the same time as peak photosynthetic rates (Fig. 3 and 7) indicates that the ET/CER ratio during rapid growth of the stands in our studies was (3.8 mmol H_2O) / (27 μmol CO_2), or ≈140 mol H_2O transpired per mole of CO_2 fixed. This is a low water-use requirement for growth in comparison with typical field values (24), but is not unexpected for the CO_2–enriched conditions used in these studies (14). In comparison, controlled environment studies by Gerbaud et al. (17) conducted at 340 μmol mol^{-1} CO_2 reported a water requirement of 300 mol H_2O per mole CO_2, a value about two times that noted in our studies.

Implications for Human Life Support in Space

At a rate of 100 L of distilled water production per day (Fig. 7) and a requirement of 18 L $person^{-1}$ d^{-1} (28), a 20-m^2 stand of wheat could adequately support the basic water need of five to six people. Obviously this would require an equal amount of water (100 L d^{-1}) restored to the nutrient solution reservoirs to sustain this evapotranspiration, but in theory this could be gray water. Thus, plant transpiration could be used as an effective water purification process for human life support.

The average CO_2 uptake rate after Day 10 for the second study equaled 18 μmol m^{-2} s^{-1}, or 26 mol CO_2 d^{-1} (for a 20-h photoperiod and 20-m^2 stand). The average respiration rate was 9μmol CO_2 m^{-2} s^{-1}, or 3 mol CO_2 d^{-1} (for a 4-h dark period). Thus a net of 23 mol CO_2 d^{-1} could be removed from a closed system by the wheat stand. Humans during space-related activities give off ≈520 L CO_2 d^{-1}, or ≈22 mol d^{-1} (28). Therefore, a 20-m^2 stand of wheat grown under similar conditions could offset the CO_2 production of ≈1.0 humans in space. If the system is closed with respect to C (e.g., no food is imported), the ultimate gas balance between the plants and humans will depend on how much of the biomass is available for human consumption. If C in the inedible biomass is to be directly recycled for reuse by the plants (e.g., by combustion or by wet oxidation), then this will decrease the portion of CO_2 removal (and O_2 production) provided during crop growth. Harvest index (seed to total biomass) values from wheat in our tests have ranged from 30 to 40%, indicating that 60 to 70% of the biomass is inedible. Thus with combustion recycling, the stand would remove CO_2 produced by only 0.3 to 0.4 humans instead of 1.0 humans, increasing the planted-area requirement from 20 m^2 to 50 m^2 per person. This represents a conservative case, since various processes might be used to convert the inedible biomass into food. For example, high-cellulase-producing fungi, such as *Trichoderma longibrachiatum* Rifai (syn. I. *reesei*), might be used to degrade the wheat straw to produce sugars for direct consumption or for feeding to other organisms, which might then be consumed. This would effectively raise the harvest index, resulting in a more favorable gas balance between humans and plants, and more efficient space utilization. Any steps to directly increase the crop harvest index would also help, and harvest indices up to 50% have been reported from controlled environment studies with wheat (5).

Ultimately, any increases in total productivity (e.g., from higher PPFD or longer photoperiods) will reduce the crop area requirements for CO_2 removal and food and oxygen production for human life support. The tradeoffs of increased energy demands must then be compared with the decrease in area and system mass requirements to determine the most economically favorable approach.

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